

# Functional anatomy of the head–neck movement system of quadrupedal and bipedal mammals

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## ABSTRACT

This biomechanical investigation quantified the range of motion of the different articulations of the head–neck ensemble in man, monkeys, cats, rabbits and guinea pigs. Radiography and dissections were used to establish the degrees of freedom of the system. The erect posture and rigidity of the cervical spine in mammalian vertebrates are possible because the degrees of freedom of the movements of the cervical and upper thoracic vertebrae in passive ranges of motion are asymmetric, and thus significantly restricted, when judged from the resting position. The total range of motion at the atlanto–occipital articulation varies between species. It is  $\sim 90^\circ$ – $105^\circ$  in the quadrupedal mammals tested, and only  $11^\circ$  or  $13^\circ$ , respectively, in humans and monkeys. When at rest, bipeds and quadrupeds hold the atlanto–occipital articulation and the upper cervical joints (C1/C2, C2/C3) in a flexed attitude. The total range of motion at the cervicothoracic junction (C6–T2) is  $\sim 6^\circ$ – $80^\circ$  in all vertebrates investigated (quadrupeds and bipeds). At rest, the vertebral articulations that form the cervicothoracic junction are held in their extreme extended positions in quadrupeds and monkeys. In man, the vertebrae of the lower cervical spine are kept at a midposition between maximal flexion and maximal extension. This latter observation may be related to the permanent bipedalism of humans. Collectively, our data indicate that biomechanical constraints such as bone structures (e.g. specifically shaped articular processes) and ligaments may maintain the intrinsic configuration and self-supporting structure of the cervical spine. Furthermore, the specialised structures in the cervical joints allow movements more or less in particular planes of space, and thus biomechanical constraints limit the number of possible solutions as to how an animal can perform a given orientating head movement. Although we have not entirely clarified the functional implications for head movement control of the different sagittal-plane ranges of motion in vertebrates, we hypothesise that different mechanical requirements relating to the influence of gravity have caused the observed differences between the investigated bipedal and quadrupedal mammals.

*Key words:* Biomechanics; posture; skull; cervical spine; vertebrae.

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## INTRODUCTION

Our previous investigations demonstrated a stereotyped resting posture of the head–neck arrangement in a number of alert and unrestrained vertebrates. The cervical vertebral column is held vertically, constituting one portion of a partial S-shaped configuration of the entire spine (Vidal et al. 1986) (see also Fig. 2A). Our subsequent investigations focused on the biomechanics of the head–neck system in different

animals in order to demonstrate the mechanical means that provide this vertical orientation. A further goal was to demonstrate the functional principles of head–neck movement control in vertebrates. The underlying hypothesis proposes that biomechanical constraints reduce the degrees of freedom of motor systems to be controlled by the nervous system. Our intent for the specific example of the cervical vertebral column was to identify areas of high or low range of motion about particular directions of movement

(flexion/extension, lateral flexion, horizontal rotation) in the context of the established resting posture of mammals (Vidal et al. 1986).

Although there are a number of studies on the biomechanics of the head-neck articulations, some of which also use radiographic analysis, most have not addressed the functional background of head movement control (Aho et al. 1955; Fielding, 1957, 1964; Jones, 1960; Bhalla & Simmons, 1969; Lysell, 1969; Suh, 1974; Brown et al. 1976; Moffat & Schulz, 1979; Dimnet et al. 1982; Goel et al. 1988; for a review, see White & Panjabi, 1990). However, for a functional interpretation of the head-neck movement system of vertebrates, or at least mammals, the ranges of motion of the different articulations have to be viewed in the context of the behaviour of alert animals (Graf & Wilson, 1989), specifically in regard to the resting position (Vidal et al. 1986). Previous studies on the biomechanics and movement strategies involved in the control of head movements have only used anaesthetised animals or postmortem material (Slijper, 1946).

Our results demonstrate that the ranges of motion of the head and neck articulations are asymmetric, based on the inherent biomechanics of the cervical and upper thoracic vertebral column when judged in the particular behavioural context of the resting posture. In essence, orientating movements of the head-neck complex in the sagittal plane that originate from the resting position involve 2 functional regions in quadrupedal mammals: the head-neck (atlanto-occipital) articulation and the cervicothoracic junction (C6-T2). Furthermore, our data suggest that quantitative changes in the range of motion of particular joints may be linked to the transition from a quadrupedal to a bipedal stance. In monkeys and adult humans, the range of motion of the atlanto-occipital articulation is significantly limited compared with quadrupeds. Thus the execution of head-neck movements in the sagittal plane in monkeys and humans is largely confined to the cervicothoracic junction and dependent primarily on this region (see Graf et al. 1995).

Preliminary accounts of this study have been published (Graf et al. 1986, 1988; Vidal & Graf, 1987; Vidal et al. 1988; Graf et al. 1992a).

## METHODS

Vertebrates studied were humans ( $n = 1$ ), monkeys ( $n = 10$ ), cats ( $n = 11$ ), rabbits ( $n = 17$ ) and guinea pigs ( $n = 12$ ). A detailed quantitative analysis using

our own material was performed in monkeys, cats, rabbits and guinea pigs. The monkey species were capucin (*Cebus apella*), rhesus (*Macaca mulatta*), cynomolgus (*Macaca fascicularis*), and squirrel monkey (*Saimiri sciureus*). All research was performed in compliance with Federal, State and University regulations and guidelines concerning the humane treatment of animals. For data about human head-neck anatomy, we limited our own experiments to 1 subject, but also used published radiographs illustrating the same experimental situations (Jeffreys, 1980; Wicke, 1980; Bland, 1987). Although much information is available in the literature about human head-neck biomechanics (see e.g. tables 2–5 of White & Panjabi, 1990), the measurements were usually not suitable for our analysis (see Discussion).

## Data acquisition

*Passive and active range of motion.* Two methods were used to determine the biomechanical characteristics (passive range of motion) of the cervical vertebral column in quadrupeds and monkeys: (1) radiographs of anaesthetised animals, and (2) direct measurements following postmortem dissection of the neck. The latter method was used primarily in rabbits (see Table 1).

In the first procedure, animals were deeply anaesthetised with a combination of ketamine (35 mg/kg), acepromazine (0.35 mg/kg) and xylazine (5 mg/kg). Their heads were fastened repeatedly in extreme positions of (ventral) flexion, (dorsal) extension and lateral flexion with masking tape. The animals were then radiographed several times at the indicated positions (Figs 2–5). This method yielded life-size images of the bony structures of interest. Selection criteria of repeat radiographs for analysis included the following: unambiguous profiles or top view exposures, sharpness of focus, extremity of investigated passive range of motion, and absence of out-of-plane complex motion (e.g. Goel et al. 1988). We obtained 20 radiographs of monkeys, 30 of cats, 31 of rabbits and 47 of guinea pigs.

In the second procedure, animals were killed by overdose of anaesthetic. The skin and muscles surrounding the upper thoracic vertebral column were removed. The bony structures to be measured were held in place at the desired end positions by mechanical devices (clamps, rods, etc). This method was especially helpful in establishing angular relationships of articulations which are difficult to assess by radiography, in particular, vertical axis rotations

Table 1. *Passive range of motion (deg) of head-neck structures in 5 rabbits (nos 1–5); direct measurements from postmortem material*

	Body weight (kg)/head weight (g)					Mean $\pm$ s.d.
	1 3.5/235	2 3.4/222	3 3.4/260	4 2.7/235	5 2.3/260	
Atlanto-occipital						
Flexion/extension	100	105	100	110	135	110.0 $\pm$ 4.6 (5)*
C7/T1						
Flexion/extension	90	80	100	65	75	82.0 $\pm$ 13.5 (5)
Lateral flexion	$\pm 15$	$\pm 5$	$\pm 12$	$\pm 12$	$\pm 15$	11.8 $\pm$ 4.1 (5)
Vertical axis rotation	0	$\pm 10$	$\pm 7$		0	4.3 $\pm$ 3.1 (4)
C1/C2/C3						
Lateral flexion	$\pm 15$ –20	$\pm 15$	$\pm 25$	$\pm 12$	$\pm 30$	20.5 $\pm$ 8.4 (5)
C1/C2						
Vertical axis rotation	$\pm 45$	$\pm 50$	$\pm 45$	$\pm 55$	$\pm 60$	51.0 $\pm$ 6.5 (5)
CVC/T1						
Flexion/extension	180	160	144	180	144	161.8 $\pm$ 18 (5)
C3/C7						
Lateral flexion	$\pm 10$	$\pm 12$	$\pm 12$	—	$\pm 25$	14.8 $\pm$ 6.9 (4)
Flexion	0	0	0	—	0	0 $\pm$ 0 (4)
Extension	15	5	10	—	5	8.8 $\pm$ 4.8 (4)

\* The number of animals is indicated throughout in parentheses.

about the odontoid process of the axis. The other measurements for flexion–extension of the head supplemented the data obtained from radiographs. However, this method was abandoned since it did not yield the required detailed intervertebral range of motion. The data are reported mainly to corroborate the results obtained by radiography.

For lateral flexion measurements, the atlanto-occipital articulation was held in an extended position to avoid out-of-plane complex motions.

For measurements in man (active range of motion) (Fig. 6), the one subject was instructed to flex, extend or bend the neck to produce the full range of movement. Four radiographs were taken. We assumed that similar instructions were given to subjects in the examples used from the published literature (Jeffreys, 1980; Wicke, 1980; Bland, 1987).

Differences between active and passive range of motion measurements are well recognised and documented, especially for data from human subjects (see e.g. White & Panjabi, 1990). In the former case, an alert animal or human holds the head as comfortably as possible. In the latter, the animal is anaesthetised or dead, and greater values for passive range of motion measurements would be expected due to the likely overextension of osseous and ligamentous structures.

*Head-neck posture in alert subjects.* To compare the passive range of motion measurements with the active head-neck posture, alert subjects were radiographed in profile view. We also reexamined radiographic

material obtained during an earlier study (Vidal et al. 1986). For data acquisition in alert animals, the same selection criteria for radiograph exposures to be accepted were applied as for anaesthetised animals. In addition, animals were required to assume the resting position. Resting position has been defined as a period of quiet stance for at least 2 min (de Beer, 1947; Vidal et al. 1986). Unfortunately, because of the great agility of monkeys, we were not able to obtain acceptable exposures in freely moving individuals of the same species. For the human subject, resting posture was thought to be established when de Beer's (1947) 'normal' position had been assumed (see also Bhalla & Simmons, 1969). In the process of this study, we took a single radiograph of the human subject, 15 of monkeys, 30 of cats, 33 of rabbits, and 19 of guinea pigs to obtain the presented results. However, the 2 test populations of the different animal species for passive range of motion and active posture measurements, respectively, overlap only partly.

#### Data analysis

Accepted radiographs were placed on a light box with an overlay of transparent paper. Either the anterior or the posterior surfaces of the bodies of the cervical and thoracic vertebrae were outlined on the transparencies. From these drawings, the angles between vertebrae relative to one another were determined using

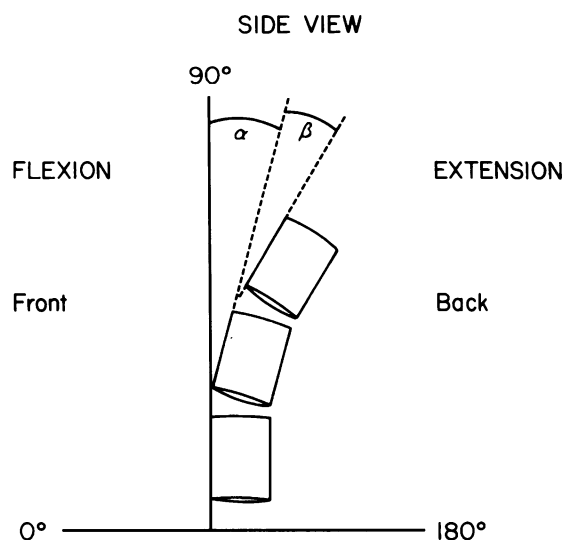


Fig. 1. Procedure for measuring vertebral orientations. Quantification of the range of motion of a given joint was accomplished by measuring the angles between the anterior surfaces of the bodies of 2 successive vertebrae (e.g.  $\alpha$ ,  $\beta$ ). For flexion, positive angles indicate bending of the cervical vertebral column in the flexion direction. For extension, positive values indicate bending of the vertebrae in the extension direction. In alert animals, the inclination of the cervical vertebral column was estimated by measuring the angle between the anterior surfaces of the vertebral bodies of given cervical or thoracic vertebrae vs the gravity vector (axis at  $90^\circ$ ) on a lateral radiograph.  $0^\circ$  corresponds to earth-horizontal.

a protractor (e.g.  $\alpha$ ,  $\beta$ , in Fig. 1). We thus measured and listed the angles formed between adjacent vertebrae during maximal flexion and maximal extension. The zero reference position for these measurements was a straight line formed by virtual alignment of the anterior or posterior surfaces of 2 neighbouring vertebrae (Fig. 1). Thus all presented measurements in anaesthetised, and several in alert animals, are relative values. The absolute ranges of motion for all measured joints can be obtained by adding the flexion and extension-direction parameters (Table 8). Separation of measured values for angular displacements into flexion and extension directions was necessary to demonstrate the context-specific positioning of particular articulations of the head-neck ensemble (see also Bhalla & Simmons, 1969). Determination of the absolute ranges of motion alone (see e.g. White & Panjabi, 1990; Selbie et al. 1993) would not supply the required data to interpret our previous observations about head-neck posture (Vidal et al. 1986; Graf et al. 1995). For lateral flexion measurements, a straight line was drawn through the centre of a given vertebra along the spinous process. As previously stated, the zero reference can be envisaged as the virtual alignment position of 2 adjacent vertebrae.

In general, all visible surfaces and reference lines were flat enough to apply a straight line, or a straight

line could easily be approximated in a repeatable fashion (Dimnet et al. 1982). In rare instances, other prominent markers had to be used to identify vertebral orientation. In such cases, the same markings were used for flexion and extension measurements; thus absolute values for range of motion were not compromised. For flexion, positive angles indicate the bending of the cervical vertebral column in the flexion direction. For extension, positive values indicate bending of the vertebrae in the extension direction.

Range of motion measurements from postmortem material of given articulations of the head-neck structures for the selected directions of movement were measured relative to one another with a goniometer. The respective points of reference were indicated by paper markers before the angle readings were taken.

In alert animals, the relative angular relationships of individual vertebrae were determined as described for anaesthetised animals (Fig. 1). Numerical values of the respective measurements in anaesthetised and alert animals are juxtaposed for comparison (Tables 2–6) and illustrated graphically (Fig. 10), and relevant radiographs are presented (Figs 2, 6). In addition, the incline and orientation of the head-neck structures versus an absolute reference position, i.e. the gravity vector (plumb line; axis at  $90^\circ$ ) or earth-horizontal ( $0^\circ$ ) on a lateral radiograph were also established (Fig. 11). The orientation in space  $\pi_i$  (in reference to earth horizontal) of a given head-neck element  $C_i$  was defined as  $\alpha(C_{i-1}[\text{space}]) - \beta(C_{i-1}/C_i) + 90 = \pi(C_i[\text{space}])$ . The zero reference  $C_0$  (head orientation) had been determined by measurement.

All the above described measurement procedures were carried out independently by different investigators for a given animal as often as necessary until all selection criteria had been met, which included positioning of the head-neck structures for passive range of motion measurements in anaesthetised and dissected animals. Individual measured values were also evaluated and reviewed by a second investigator to ensure accuracy. Discrepancies in measured values that warranted reexamination of the original material occurred only for guinea pigs because of the small size of the structures and the low radiodensities involved.

As already mentioned, angular measurements are presented as flexion or extension angles, i.e. positive values indicate an angular displacement resulting in more flexion or extension (see Tables 2–6). Negative values would signal a displacement in the opposite direction. For example, although a certain degree of flexion is expected and present, a particular measured value may indicate extension; see e.g. Tables 5 and 6,

2nd and 1st columns, respectively). Such displacements in the opposite direction are known as paradoxical motions and may be associated with instability (White & Panjabi, 1990). In the majority of cases, a value of 'opposite sign', however, does not indicate movement in the opposite direction, but does represent the relative position of a measurable structure which can easily be reproduced. Wherever applicable, these will be specifically pointed out.

Head orientation in rabbits, guinea pigs and cats is referenced to horizontal semicircular canal orientation. In guinea pigs and rabbits, the horizontal semicircular canal forms a 123° angle with the tangent of the nasal bone (Curthoys et al. 1975; Hughes, 1981; Ezure & Graf, 1984). In cats, horizontal semicircular canal orientation is in the plane of a line connecting the external auditory meatus and the rostral tip of the frontal sinus (Vidal et al. 1986). In humans and monkeys, the Frankfurt plane served as the head reference. Where appropriate, the orientation of the horizontal semicircular canals is also indicated. These 2 reference planes form an anteriorly open angle with the canal plane tilted upwards from the Frankfurt plane. The relationship between the 2 parameters is 25° in man (Blanks et al. 1975), and 22° in adult rhesus monkeys (Blanks et al. 1985).

All values were averaged and standard deviations were calculated according to standard statistical methods and are presented as such, with the exception of Table 1 (direct measurements from postmortem material).

## RESULTS

Analysis of the range of motion of the head-neck joints was performed predominantly by using radiographs and direct measurements from postmortem dissections.

### *Rabbits*

In rabbits, a detailed analysis of the biomechanical characteristics of the head-neck articulations was performed using direct measurements and measurements from radiographs. Direct measurements in small animals were suited for global determinations of range of motion involving entire functional compartments, whereas the radiograph measurements allowed single-joint analysis (compare Tables 1 and 2).

Direct measurements from postmortem dissections indicate an average range of motion for flexion/

extension movements of 110° at the atlanto-occipital articulation, and of 82° at the cervicothoracic junction (C6/T2). The value for lateral flexion of the cervical spine is about  $\pm 20^\circ$ , primarily occurring at C1/C2/C3 (Table 1). The values for rotation about the vertical axis indicate 2 additive components providing approximately 180° range of motion from maximal left turn to maximal right turn ( $\pm 90^\circ$  excursion). About 50% of this range occurs at C1/C2 (about the odontoid process, i.e. dens axis); the remaining 50% must be allocated to vertical axis rotations of the cervical vertebrae relative to one another (see also Fielding, 1964; Crisco et al. 1991). There is little vertical axis rotation at C7/T1 (Table 1). The segments between C3 and C7 do not allow major excursions in any direction (Table 1; see also Fig. 7).

Measurements from radiograph images (Fig. 2) corroborate the findings obtained from the direct measurements. The average total range of motion for flexion/extension of the head at the atlanto-occipital articulation obtained by this method is approximately 100° (Table 2) compared with 110°, when direct measurements are used (Table 1).

The single-joint measurements also indicate that noticeable excursions for flexion appear only between C2/C3 and C3/C4, whereas all the other joints largely allow only deviations in the extension direction (Table 2). Limited lateral flexion of the cervical vertebral column in the rabbit is possible from C1 to C5 (Table 9, 1st column).

Comparison of data for the passive range of motion of the head-neck structures with that obtained from alert unrestrained animals at the resting position reveals how rabbits hold their heads while at rest (Figs 2, 10; Table 2). The 2 data sets indicate that the atlanto-occipital articulation and the C1/C2 joint are held at their maximally flexed positions when the animal is at rest (e.g. 109° vs 114° to the atlanto-occipital articulation, and 0.4° when 21.8° of extension would be possible at C1/C2; also note the limitation of 0.7° in the flexion direction at the latter joint). The close correspondence of these numerical values becomes even more remarkable since the data were obtained from 2 different animal populations. Below C3/C4, the vertebrae are brought to the end points of their extension positions. Thus, at rest, the lower cervical vertebral column is held in a maximally extended attitude. From this position, the articulations at the cervicothoracic junction (C6-T2), involving several vertebrae of the lower cervical and the upper thoracic vertebral column, can only move in the flexion direction (compare Fig. 2A with 2B, and 2A with 2C).

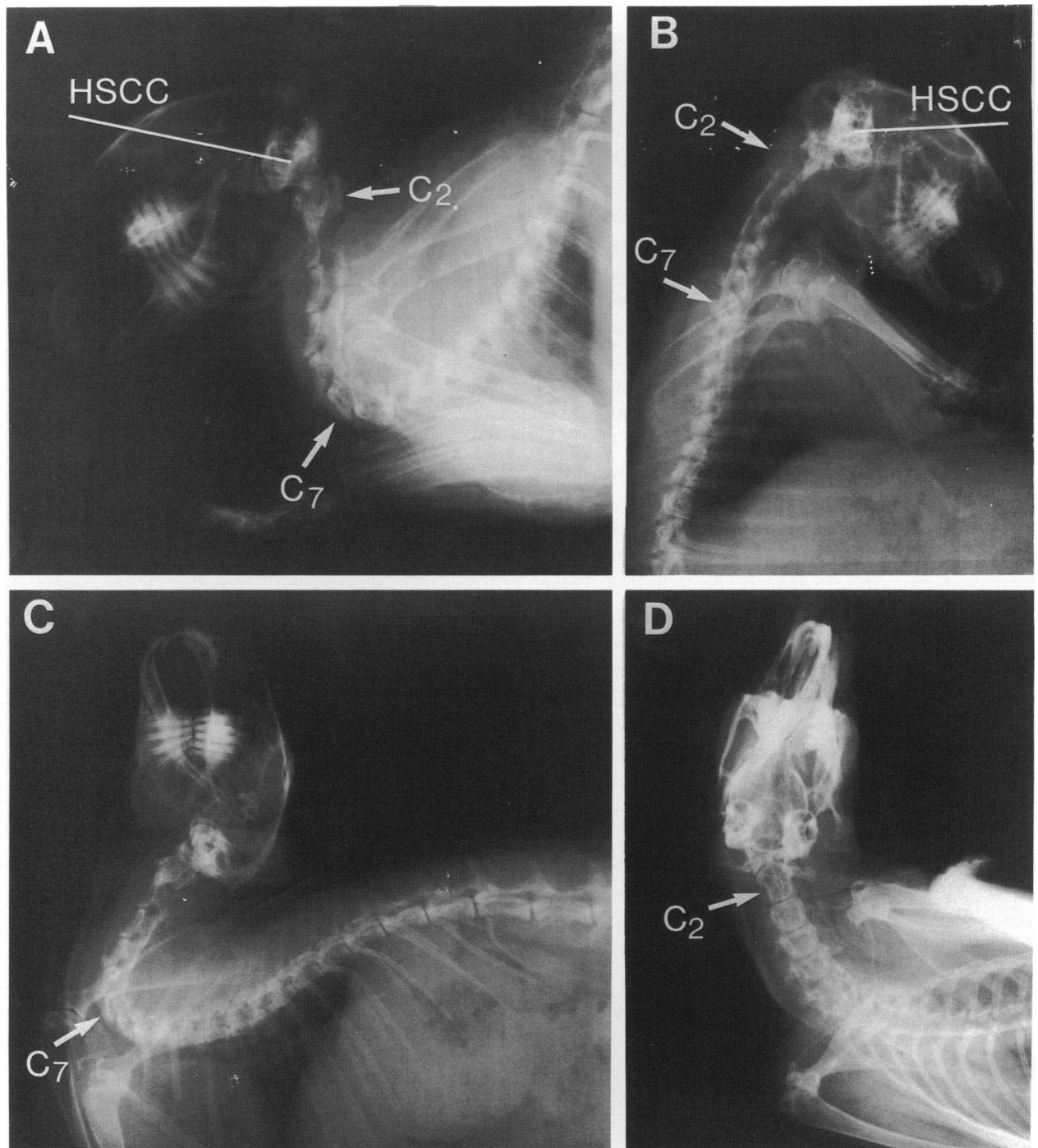


Fig. 2. Head-neck posture and passive range of motion of the head-neck joints in rabbits. Radiographs of an alert (*A*) and anaesthetised animal (*B–D*) (same individual). *A*, resting position; *B*, maximal flexion; *C*, maximal extension; *D*, maximal lateral flexion. Note similar excursions of degree of flexion at the atlanto-occipital articulation in *A* and *B*. To illustrate this similarity, the exposure in *B* was oriented in such a way as to make the cervical spine approximately orientated vertically. However, in the passive range of motion experiment, a noticeable flexion between C3 and C4 is present. Also note approximate similar horizontal canal orientation in *A* and *B*, and similar extension at the cervicothoracic junction in *A* and *C*. HSCC, horizontal semicircular canal plane.

The results shown in Table 7 (1st column) confirm our previous observations (Vidal et al. 1986) at the single vertebra level that rabbits hold their cervical vertebral column vertically when at rest (indicated by the values close to 90° for C1–C4; see also Fig. 11).

The values below C5 signal the curvature of the cervicothoracic junction. In this particular position, rabbits maintain the horizontal semicircular canals tilted upwards from earth horizontal by about 16° (see also Vidal et al. 1986; Graf et al. 1995).

Table 2. *Passive range of motion (flexion and extension directions) and active positioning at rest of the head-neck articulations in rabbits (deg, mean  $\pm$  S.D.)*

	Passive range of motion		Alert (at rest) Extension direction
	Flexion	Extension	
Head/C1	114.3 $\pm$ 13.5 (6)	-14.3 $\pm$ 4.1 (6)	-109.6 $\pm$ 7.6 (9)
C1/C2	0.7 $\pm$ 1 (6)	21.8 $\pm$ 3.7 (6)	0.4 $\pm$ 2.9 (9)
C2/C3	11.3 $\pm$ 1.9 (6)	3.7 $\pm$ 4 (6)	-1.0 $\pm$ 7.7 (9)
C3/C4	11.8 $\pm$ 3.4 (6)	7.0 $\pm$ 4.4 (6)	-3.4 $\pm$ 6.5 (9)
C4/C5	5.0 $\pm$ 2.6 (6)	18.1 $\pm$ 7.2 (6)	6.1 $\pm$ 8.5 (9)
C5/C6	2.0 $\pm$ 2.1 (6)	28.0 $\pm$ 8.3 (6)	20.7 $\pm$ 4.5 (9)
C6/C7	3.4 $\pm$ 5.5 (6)	33.8 $\pm$ 5 (6)	26.8 $\pm$ 7.7 (9)
C7/T1	0.7 $\pm$ 2.4 (6)	24.7 $\pm$ 11.4 (6)	31.1 $\pm$ 9.1 (9)
T1/T2	1.7 $\pm$ 2.3 (6)	16.2 $\pm$ 8.7 (6)	—
T2/T3	1.2 $\pm$ 2.7 (5)	5.3 $\pm$ 4.7 (6)	—
T3/T4	0 (2)	5.0 $\pm$ 3.7 (4)	—

For passive range of motion, note that the greater values in the flexion direction occur predominantly at the upper cervical level. Greater values in the extension direction appear at the lower cervical and upper thoracic level. The angular positions of these same vertebral joints in unrestrained alert animals are presented in the extension direction. Note that animals hold their head-neck systems at maximal flexion in the upper cervical column (Head/C1, C1/C2), and close to maximal extension in the lower cervical and upper thoracic column (C4/C5 to C7/T1). Since the angles for the unrestrained rabbits are given for the direction of extension, the values for Head/C1 and C3/C4 indicate flexion. The horizontal semicircular canals served as the head reference. Note the general asymmetry of low flexion angles in the lower cervical column, but the high mobility in the extension direction. The data indicate a compartmentalisation of the cervical spine with regard to the areas where flexion and also where extension movements may take place as judged from the resting position.

### Guinea pigs

Data on the articular range of motion of the cervical vertebrae in the guinea pig are illustrated in Figure 3 and summarised in Table 3.

Individual measurements of passive range of motion indicate that only the C1/C2 joint allows noticeable excursions in the flexion direction. Displacements in the extension direction largely involve the lower cervical and upper thoracic spine. The average range of motion of the atlanto-occipital articulation in the sagittal plane is 106° (see also Tables 8, 10).

Lateral flexion within the cervical spine in the guinea pig is limited. Direct measurements of lateral flexion indicated a total average passive range of motion of  $\pm 18^\circ$  ( $n = 2$ ). Measurements from radiographs show a similar excursion range (Table 9, 2nd column).

Postmortem dissections also determined the extent of vertical axis rotation of the head. A total range of motion of 170° was found. The atlanto-axial joint contributed 94° to this range ( $n = 1$ ).

When comparing passive range of motion with the head-neck posture adopted by alert guinea pigs at rest (Table 3; Fig. 10), we again observed that the atlanto-occipital articulation is held positioned at its limit in the flexion direction (120° vs 112°). In a similar fashion, the upper 2 cervical joints (C1/C2 and C2/C3) are also brought into a flexed attitude. Below the C3/C4 articulation, the cervical vertebrae are held in extreme extension positions.

While at rest, guinea pigs also keep their horizontal semicircular canals tilted upwards from earth horizontal (by about 20°) as observed previously (Vidal et al. 1986) (Table 7, 2nd column; Fig. 11). The vertical orientation of the cervical spine is illustrated by the close to 90° orientations of vertebrae C1–C4. Below C5, the curvature of the cervicothoracic junction is beginning (Fig. 11).

### Cats

Passive range of motion measurements in cats outline the same tendencies as shown in rabbits and guinea pigs. Results are illustrated in Figure 4, and detailed numerical values are summarised in Table 4. The average range of motion at the atlanto-occipital articulation in cats is about 92° (Tables 8, 10). There is a low capacity in the cervical spine for flexion, except at the C2/C3 articulation. Although our data have been averaged, this particular cat-specific joint is still prominently noticeable (Fig. 11) (Vidal et al. 1986; Graf et al. 1995). Its possible functional implications will be discussed in a separate section below. Excursions in the extension direction occur throughout the cervical spine except for C2/C3. Limited lateral flexion of the cervical vertebral column is only possible between C1 and C2 (Table 9, 3rd column).

When judged from the resting position of alert animals (Table 4; Fig. 10), the atlanto-occipital articulation (111° vs 108°) and the vertebral joints C1/C2, C2/C3 and C3/C4 appear maximally flexed. The closeness in numerical values is particularly noteworthy for C1/C2 (1.7° of flexion vs 3.2° of flexion when 14.4° of extension would be possible), and for C2/C3 (18.7° of flexion vs 10.2° of flexion). The joints of the lower spine are held in maximally extended positions.

Absolute orientations of the head-neck joints indicate the previously observed upward tilt of the horizontal semicircular canal plane (20°) and a close to vertical orientation of vertebrae C1–C5. The orientation of C6 to T1 signals the curvature of

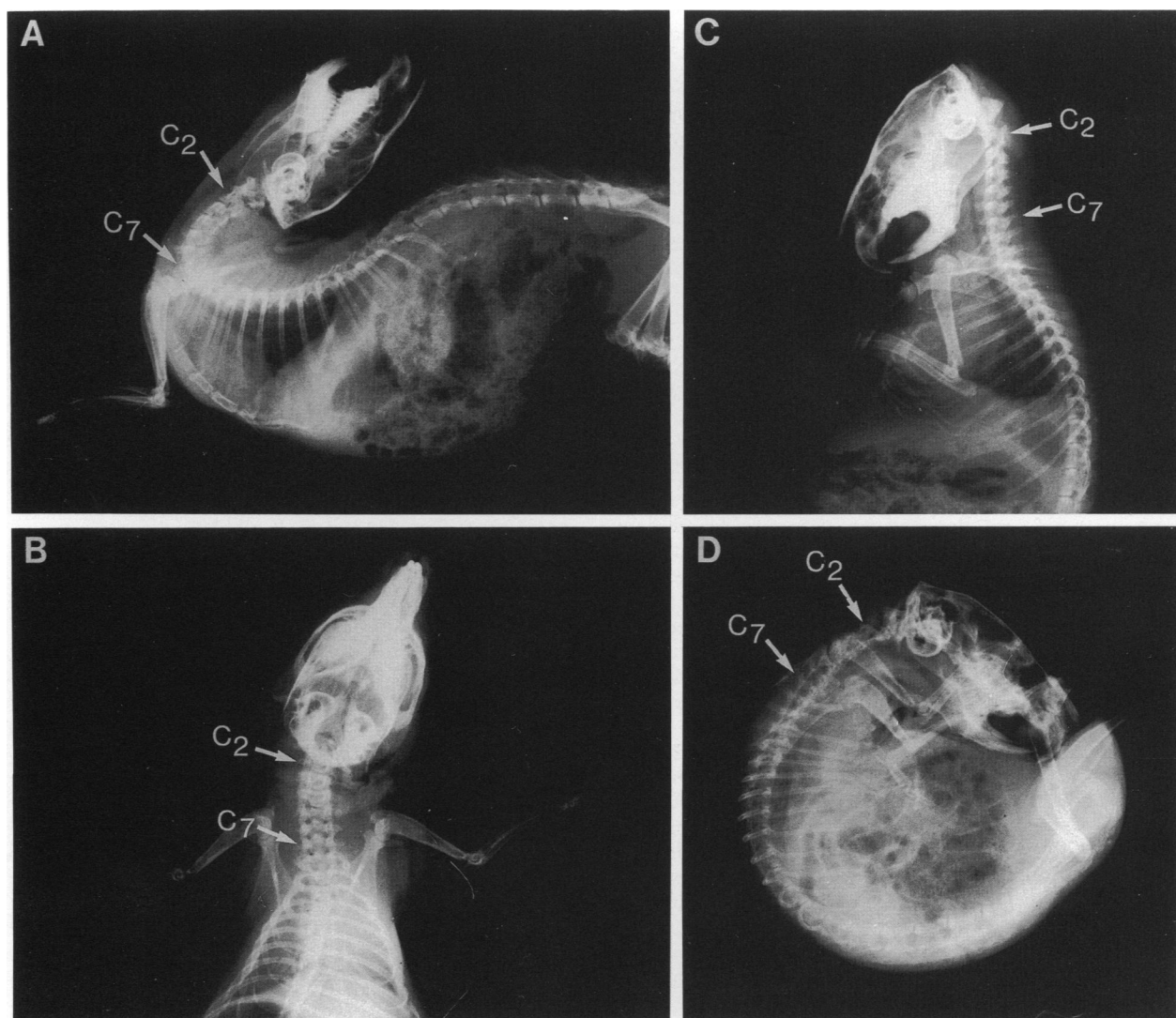


Fig. 3. Passive range of motion of the articulations of the head-neck structures in guinea pigs. Radiographs in *A*, maximal extension; *B*, maximal lateral flexion; *C*, flexion (atlanto-occipital articulation); *D*, flexion (entire cervical vertebral column). Note predominant low mobility in the middle cervical spine, and large flexion-extension range of motion at its upper and lower portions.

the cervicothoracic junction (Table 7, 3rd column; Fig. 11).

### Monkeys

Passive range of motion measurements were undertaken in 3 monkey species: rhesus (*Macaca mulatta*), cynomolgus (*Macaca fascicularis*) and squirrel monkey (*Saimiri sciureus*) (Fig. 5, Table 5). Data from these 3 species are essentially similar, with the exception of a lack of indicated flexion between C2/C3 in the squirrel monkeys, and a possible paradoxical motion during flexion between C1/C2 in cynomolgus. As a general tendency, we observed that movements in the flexion direction seem to be even more restricted than in the quadrupedal mammals introduced above, except for the C2/C3 joint in

rhesus and cynomolgus monkeys. The range of motion in the extension direction shows values comparable to the data presented for the investigated quadrupeds, in general, indicating little range of motion in the upper cervical column, and allowing larger excursions in the lower part of the cervical spine. Most significantly, the range of motion of the atlanto-occipital articulation is significantly reduced compared with rabbits, cats and guinea pigs (Table 8). Across the available measurements, the average is only 13° (Table 10). Lateral flexion is significantly restricted in the entire cervical column in the 2 tested species (Table 9, 4th and 5th columns).

Unfortunately, we were unable to obtain acceptable still radiographs in an alert and freely moving monkey of the same species. Our measurements from an alert capucin monkey when compared with values obtained

Table 3. *Passive range of motion (flexion and extension directions) and active positioning at rest of the head-neck articulations in guinea pigs (deg, mean  $\pm$  s.d.)*

	Passive range of motion		Alert (at rest) Extension direction
	Flexion	Extension	
Head/C1	120.2 $\pm$ 8.1 (5)	-14.4 $\pm$ 3.5 (5)	-112.3 $\pm$ 10.4 (5)
C1/C2	23.8 $\pm$ 5.1 (6)	13.8 $\pm$ 3.3 (5)	-3.7 $\pm$ 5.0 (6)
C2/C3	4.2 $\pm$ 4 (6)	2.8 $\pm$ 1.3 (5)	-2.3 $\pm$ 2.6 (6)
C3/C4	0 $\pm$ 0 (6)	13.4 $\pm$ 1.8 (5)	4.0 $\pm$ 6.2 (6)
C4/C5	0 $\pm$ 0 (6)	9.6 $\pm$ 1.5 (5)	15.2 $\pm$ 3.1 (6)
C5/C6	0 $\pm$ 0 (6)	17.2 $\pm$ 1.9 (5)	20.8 $\pm$ 13.5 (6)
C6/C7	—	21.8 $\pm$ 2.4 (5)	27.8 $\pm$ 7.1 (6)
C7/T1	—	21.5 $\pm$ 1.3 (4)	22.8 $\pm$ 11.6 (6)
T1/T2	—	17.7 $\pm$ 3.8 (3)	—

For passive range of motion, note that the greater values in the flexion direction occur at the extreme upper cervical level. The greater values in the extension direction appear almost throughout the entire cervical and upper thoracic level. The value for extension at Head/C1 appears negative (-), because the angle appears as 'flexion' (see Methods). In this case, the value does not denote paradoxical motion, but the relative angle between a conveniently placed measurable radiodense structure and the horizontal semicircular canal orientation. In alert unrestrained animals at rest, the upper cervical column (Head/C1 to C2/C3) is held in flexion (signified by the minus sign), largely at the end points of the passive range of motion, whereas the lower cervical and upper thoracic column (C4/C5 to C7/T1) are held in maximal extension. The horizontal semicircular canals served as the head reference. Note the general asymmetry of low flexion angles in the lower cervical column, but the high mobility in the extension direction. The data indicate a compartmentalisation of the cervical spine with regard to the areas where flexion and extension movements may take place as judged from the resting position.

from squirrel monkeys (individual animals of these 2 species were about the same size) nevertheless indicate the previously observed flexed attitude of the upper cervical column, including the atlanto-occipital articulation (107° vs 108°), and an extended positioning of lower cervical vertebrae (Table 5; Fig. 10).

Absolute orientations of the head-neck elements again indicate an upwardly tilted semicircular canal plane (12°) and, quite in contrast to the quadrupedal mammals, a forward-leaning attitude of all cervical

Table 4. *Passive range of motion (flexion and extension directions) and active positioning at rest of the head-neck articulations in cats (deg, mean  $\pm$  s.d.)*

	Passive range of motion		Alert (at rest) Extension direction
	Flexion	Extension	
Head/C1	111.3 $\pm$ 10.1 (3)	-19.4 $\pm$ 11 (3)	-108.0 $\pm$ 5.9 (5)
C1/C2	1.7 $\pm$ 2.9 (3)	14.3 $\pm$ 2.5 (3)	-3.2 $\pm$ 3.8 (5)
C2/C3	18.7 $\pm$ 5.5 (3)	1.3 $\pm$ 2.3 (3)	-10.2 $\pm$ 11.0 (5)
C3/C4	9.7 $\pm$ 1.5 (3)	9.0 $\pm$ 2.6 (3)	-3.0 $\pm$ 6.7 (5)
C4/C5	6.7 $\pm$ 7 (3)	17.0 $\pm$ 2.6 (3)	16.4 $\pm$ 6.0 (5)
C5/C6	1.0 $\pm$ 1 (3)	21.3 $\pm$ 3.5 (3)	14.0 $\pm$ 9.7 (5)
C6/C7	0.4 $\pm$ 0.6 (3)	26.7 $\pm$ 3.8 (3)	21.1 $\pm$ 6.3 (5)
C7/T1	1.4 $\pm$ 1.5 (3)	22.7 $\pm$ 7.5 (3)	24.6 $\pm$ 5.9 (5)
T1/T2	0 $\pm$ 0 (3)	13.3 $\pm$ 2.1 (3)	—
T2/T3	—	14.3 $\pm$ 4.2 (3)	—
T3/T4	—	12.3 $\pm$ 2.5 (3)	—
T4/T5	—	10.3 $\pm$ 7.6 (3)	—
T5/T6	—	7.7 $\pm$ 5.7 (3)	—

For passive range of motion, note that the greater values in the flexion direction occur predominantly at the upper cervical level. The greater values in the extension direction appear at the lower cervical and upper thoracic level. The value for extension at Head/C1 is negative (-) because the angle appears as 'flexion' (see Methods). This value does not denote paradoxical motion, but the relative angle between a conveniently placed measurable and radiodense structure and the indicator for horizontal semicircular canal orientation. In alert unrestrained animals at rest, the upper cervical column (Head/C1 to C3/C4) is held in flexion (signified by the minus sign) largely at the end points of the passive range of motion, whereas the lower cervical and upper thoracic column (C4/C5 to C7/T1) are held in maximal extension. The horizontal semicircular canals served as the head reference. Note the general asymmetry of low flexion angles in the lower cervical column, but the high mobility in the extension direction. The data indicate a compartmentalisation of the cervical spine with regard to the areas where flexion and extension movements may take place as judged from the resting position.

vertebrae, and thus of the entire cervical spine (Table 7, 4th column; Fig. 11).

### Man

All values resulted from active range of motion measurements (Fig. 6, Table 6). As in the monkeys,

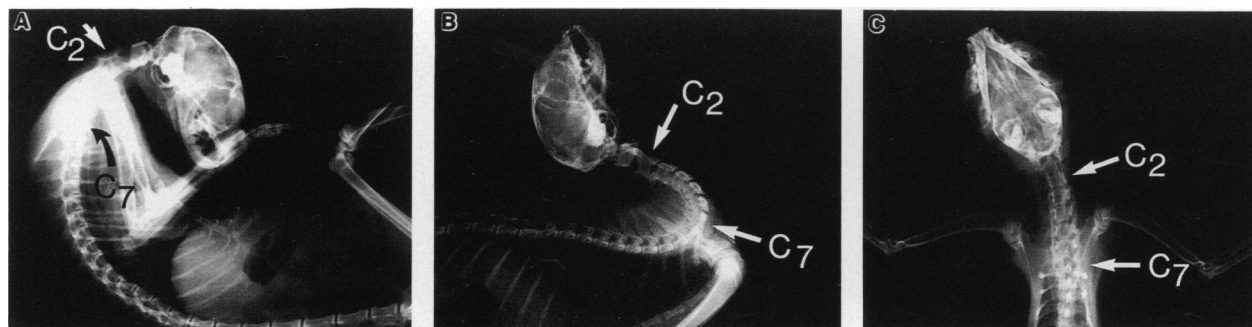


Fig. 4. Passive range of motion of the head-neck joints in cats. *A*, maximal flexion; *B*, maximal extension; *C*, maximal lateral flexion. Large flexion-extension movements are possible at the upper cervical column and at the cervicothoracic junction (around C7). There is also noticeable mobility in the flexion direction at the C2/C3 articulation in cats.

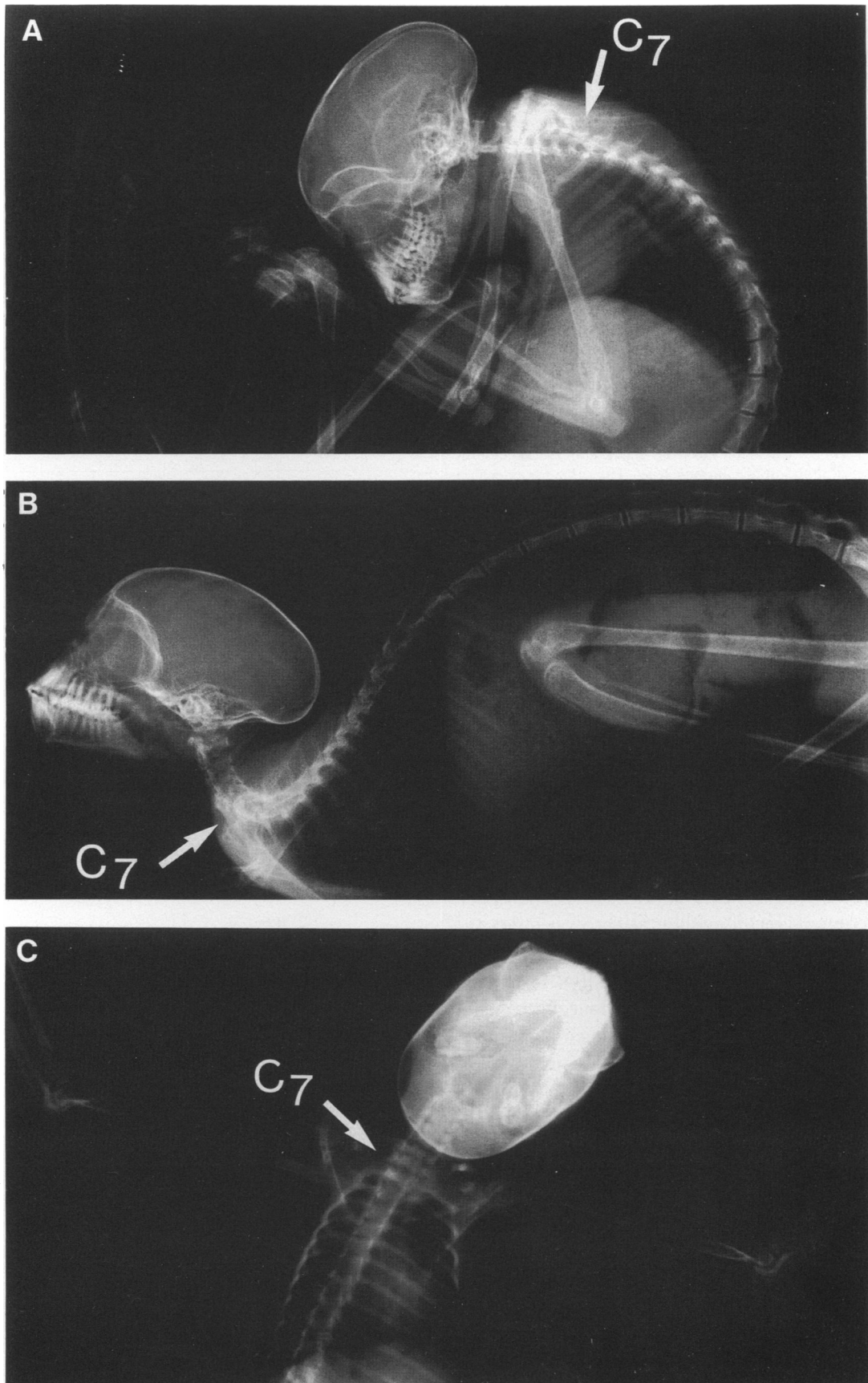


Fig. 5. Passive range of motion of the head-neck joints in squirrel monkeys. *A*, maximal flexion; *B*, maximal extension; *C*, maximal lateral flexion. Note greatest mobility for flexion-extension at the cervicothoracic junction (around C7). There is little mobility throughout the entire cervical spine, and the range of motion of the atlanto-occipital articulation is rather restricted.

Table 5. Passive range of motion (flexion and extension directions) in rhesus (*M. mul.*), cynomolgus (*M. fasc.*) and squirrel monkeys (*S. sci.*) and active positioning at rest of the head-neck articulations in a capucine monkey (*C. ape.*) (deg, mean  $\pm$  s.d.)

Passive range of motion							Alert, at rest Extension direction <i>C. apella</i>
Flexion			Extension				
<i>M. mul.</i>	<i>M. fasc.</i>	<i>S. sci.</i>	<i>M. mul.</i>	<i>M. fasc.</i>	<i>S. sci.</i>		
Head/C1	105	118. ± 10.1 (3)	106.7 ± 20.2 (3)	− 137	− 119.3 ± 5.1 (3)	− 116.4 ± 12.3 (5)	− 107.5 (2)
C1/C2	0	− 5.3 ± 2.1 (3)	3.3 ± 5.8 (3)	3	7.0 ± 2.6 (3)	22.2 ± 9.4 (5)	0 (2)
C2/C3	20	18.3 ± 6.7 (3)	0.7 ± 0.6 (3)	4	16.0 ± 4.6 (3)	3.6 ± 2.3 (5)	0 (2)
C3/C4	4	5.0 ± 5.6 (3)	4.7 ± 5.0 (3)	10	8.7 ± 1.5 (3)	8.6 ± 2.6 (5)	1.5 (2)
C4/C5	5	0 ± 0 (3)	3.7 ± 4.7 (3)	13	11.3 ± 4.2 (3)	11.2 ± 2.3 (5)	0 (2)
C5/C6	0	0 ± 0 (3)	3.7 ± 0.6 (3)	16	8.6 ± 3.2 (3)	12.0 ± 4.0 (5)	2.5 (2)
C6/C7	0	0 ± 0 (3)	3.0 ± 1.7 (3)	22	16.7 ± 5.7 (3)	19.0 ± 1.6 (5)	20.5 (2)
C7/T1	0	—	3.0 ± 1.7 (3)	10	21.3 ± 7.0 (3)	22.6 ± 8.3 (5)	6.5 (2)
T1/T2	6	—	5.7 ± 3.5 (3)	20	17.3 ± 5.1 (3)	16.0 ± 2.2 (5)	
T2/T3	1	—	8.7 ± 5.7 (3)	0	10.3 ± 5.5 (3)	10.4 ± 5.0 (5)	
T3/T4	5	—	6.7 ± 2.9 (3)	—	4.6 ± 5.7 (3)	6.0 ± 5.8 (5)	
T4/T5	1	—	—	—	—	—	

In rhesus monkeys only 1 set of measurements was taken. For passive range of motion, note that the greater values in the flexion direction occur predominantly at the upper cervical level. The greater values in the extension direction appear at the lower cervical and upper thoracic level. The values for extension at Head/C1 are negative (—), because the angles appear as 'flexion' (see Methods). These values do not denote paradoxical motion, but the relative angles between conveniently placed measurable and radiodense structures and the Frankfurt plane. By contrast, the C1/C2 value in *M. fasc.* may signal paradoxical motion. In an alert unrestrained monkey at rest (*C. ape.*), the upper cervical column (Head/C1 to C5/C6) is held in flexion (signified by the minus sign), largely at the end points of the passive range of motion, whereas the lower cervical and upper thoracic column (C6/C7 to C7/T1) are held in extension. The Frankfurt plane served as the head reference. Note the general asymmetry of low flexion angles in the lower cervical column, but the high mobility in the extension direction. The data indicate a compartmentalisation of the cervical spine with regard to the areas where flexion and extension movements may take place as judged from the resting position.

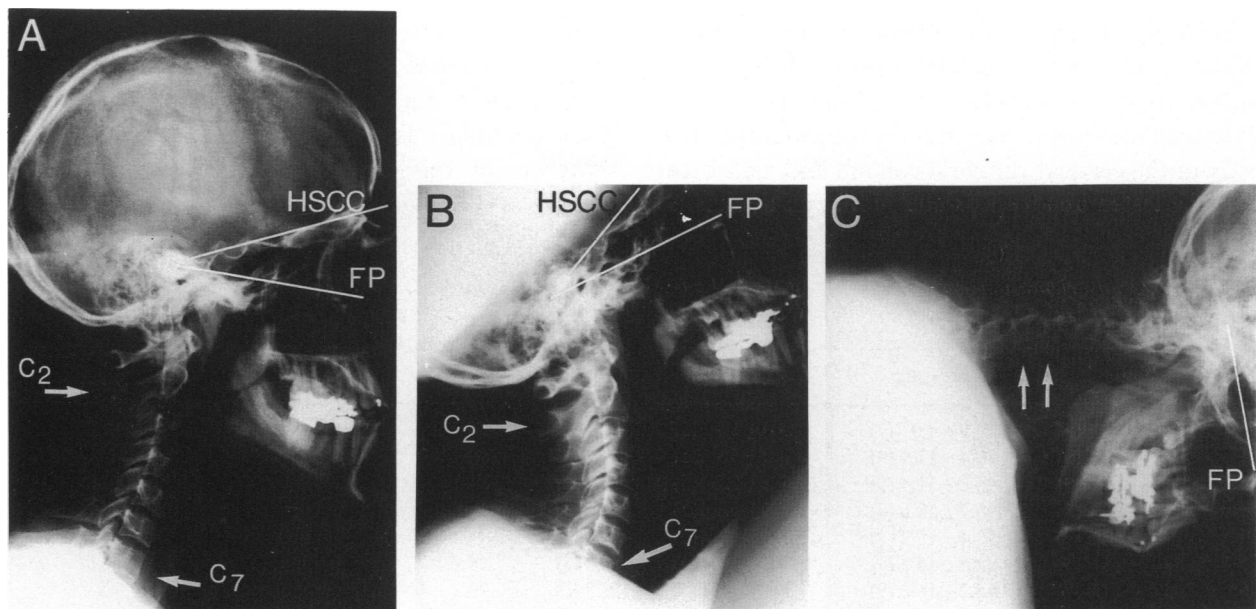


Fig. 6. Head-neck posture and active range of motion of the head-neck joints in man. *A*, resting position; *B*, extension; *C*, flexion. Note upward orientation of the horizontal semicircular canals at resting position, and limited extension mobility from the resting position compared with flexion excursion. Note sliding of vertebrae against one another during flexion (arrows in *C*, pointing at the 5th and 6th cervical vertebrae, C5–C6). FP, Frankfurt plane; HSCC, horizontal semicircular canal plane.

the range of motion of the atlanto-occipital articulation in our subject (11°;  $n = 1$ ) was also limited compared with the tested quadrupeds (see also Table

10). As a general tendency, flexion excursions seemed to be restricted at the upper cervical spine, but not at the lower cervical level. This latter finding is quite

Table 6. *Active range of motion (flexion and extension directions) and positioning of the head-neck articulations at rest in man (deg, mean  $\pm$  S.D.)*

	Active range of motion				At rest Extension direction
	Flexion		Extension		
Head/C1	90	(1)	-101	(1)	-90
C1/C2	5.0 $\pm$ 4.3	(4)	4.8 $\pm$ 4.7	(5)	1
C2/C3	-0.25 $\pm$ 4.5	(4)	10.4 $\pm$ 7.4	(5)	6
C3/C4	2.25 $\pm$ 2.2	(4)	10.2 $\pm$ 6.4	(5)	5
C4/C5	6.75 $\pm$ 1.7	(4)	12.4 $\pm$ 2.1	(5)	4
C5/C6	8.75 $\pm$ 4.3	(4)	15.4 $\pm$ 6.8	(5)	1
C6/C7	12.0 $\pm$ 4.2	(4)	8.6 $\pm$ 3.5	(5)	0
C7/T1	15	(1)	—		0

For resting posture, only the set of measurements obtained from our own subject was entered. Flexion is restricted at the upper cervical level (negative flexion values for C1/C2 and C2/C3), but possible at the lower cervical articulations. Extension can occur throughout all compartments. When the subject is at rest, the atlanto-occipital articulation is held at the extreme flexed position. All other vertebrae are held in an extended posture but more or less at the midpoints of their range of motion. The Frankfurt plane served as the head reference.

different from all other mammals tested, and suggests important biomechanical differences affecting the intrinsic configuration of the cervical spine and, ultimately, how head-neck movements are executed in humans. In fact, the larger flexion excursions (12° and 15°) at the lower vertebrae (C6/C7 and C7/T1, respectively) reflect a linear forward motion, so-called 'sliding', of these structures across their curved surfaces (Graf et al. 1990, 1992c; Wang et al 1991). Extension movements can occur throughout the main body of the cervical vertebral column and, consistent with the tested quadrupeds and monkeys, there is no

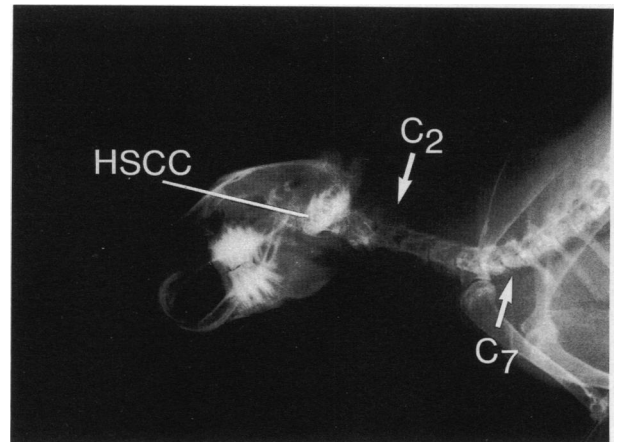


Fig. 7. Lateral radiograph of an alert behaving rabbit showing exploratory behaviour. Note head orientation that shows little deviation from the resting position of the animal and straight configuration of the cervical vertebral column. In this particular instance, the head-neck ensemble is used in a parallelogram fashion in concert with the cervicothoracic junction and the thoracic vertebral column. Head orientation in the sagittal plane is controlled independently of cervical column orientation (compare with Fig. 9B, where the monkey holds the cervical spine oriented at approximately the same angle, but achieves a different head posture). HSCC, horizontal semicircular canal plane.

significant lateral flexion excursion (Table 9, 6th column).

When radiographic data from the literature were analysed, it was difficult to estimate the instructions that had been given to a subject regarding the degree of flexion or extension of the neck. In any case, the subsequently obtained measurements showed the same tendencies as in our subject. The comprehensive synopsis of cervical spine rotations by White & Panjabi (1990) indicated considerable variability in

Table 7. *Spatial orientation and positioning of individual vertebrae (deg, mean  $\pm$  S.D.) for the studied alert vertebrates when at rest*

	Rabbit	Guinea pig	Cat	<i>C. apella</i>	Man
HSCC	15.9 $\pm$ 5.7 (9)	19.9 $\pm$ 4.9 (7)	20.0 $\pm$ 6.1 (5)	12.0 (2)	22
C1	86.3 $\pm$ 9.9 (9)	89.4 $\pm$ 11.9 (9)	88.0 $\pm$ 5.9 (5)	62.5 (2)	80
C2	85.9 $\pm$ 11.8 (9)	95.8 $\pm$ 11.5 (9)	91.2 $\pm$ 5.2 (5)	62.5 (2)	84
C3	86.9 $\pm$ 11.5 (9)	96.7 $\pm$ 12.6 (9)	101.4 $\pm$ 6.1 (5)	62.5 (2)	75
C4	90.3 $\pm$ 16.3 (9)	93.4 $\pm$ 15.2 (9)	104.4 $\pm$ 11.7 (5)	61.0 (2)	76
C5	84.2 $\pm$ 18.0 (9)	82.8 $\pm$ 15.3 (9)	88.0 $\pm$ 16.4 (5)	61.0 (2)	78
C6	63.6 $\pm$ 19.9 (9)	62.2 $\pm$ 16.2 (9)	74.0 $\pm$ 19.8 (5)	58.5 (2)	76
C7	35.7 $\pm$ 20.1 (9)	34.5 $\pm$ 17.2 (9)	52.8 $\pm$ 9.6 (5)	38.0 (2)	75
T1	4.5 $\pm$ 20.2 (9)	7.0 $\pm$ 21.1 (8)	28.2 $\pm$ 10.7 (5)	31.5 (2)	—

For man, only the set of measurements obtained from our own subject is entered. The relative 'at rest' angles of Tables 2–6 were converted to reflect absolute orientation in reference to each horizontal (see Methods). An orientation of 0° denotes earth horizontal; a value of 90° indicates the direction of gravity (see also Fig. 1). Thus the vertebral orientations of the upper cervical column appear close to 90°, indicating vertical orientation. Smaller values indicate forward orientation, higher values backward orientation. Decreasing values in quadrupeds (from about C6 on) indicate the beginning of the first curvature of the partial S-shape of the entire vertebral column. Monkeys and humans hold their cervical vertebrae in a slightly forward-inclined position. In all instances, the head is held with the horizontal semicircular canals (HSCC) tilted upwards from each horizontal.

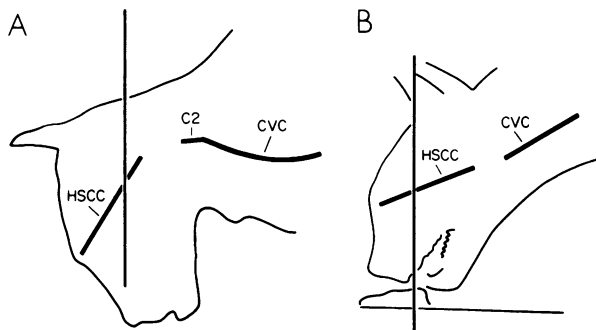


Fig. 8. Head-neck orientation in an alert unrestrained cat during extreme positions of gaze. A, looking down; B, eating; HSCC, horizontal semicircular canal. Note straight configuration of the cervical vertebral column (CVC). Vertical bars indicate direction of gravity.

the biomechanical data, depending on investigators, subjects, conditions and methods used (see their tables 2–5, p. 110). In our own example, the flexion of the neck at the cervicothoracic junction was far more pronounced than shown in most other publications.

Comparison of data between range of motion of vertebral articulations and vertebral positions at rest also indicates that humans hold the atlanto–occipital articulation in a flexed attitude, whereas the upper cervical joints are held in slightly extended positions. The lower cervical vertebrae are kept at a midposition between maximal flexion and maximal extension (Fig. 10). Given the total range of motion, in particular of the lower cervical vertebrae in the flexion direction, this particular part of the cervical spine must be maintained actively at the approximate midposition.

Our data on the absolute orientation of the cervical vertebrae show that humans also keep their cervical spine in a forward leaning attitude when assuming the resting posture similar to monkeys but, again, this is quite in contrast to the situation observed in quadrupeds (Table 7, 5th column; Fig. 11). As in all other tested vertebrates, the horizontal semicircular canal plane is kept tilted upwards (in this case, by 22°; Fig. 11).

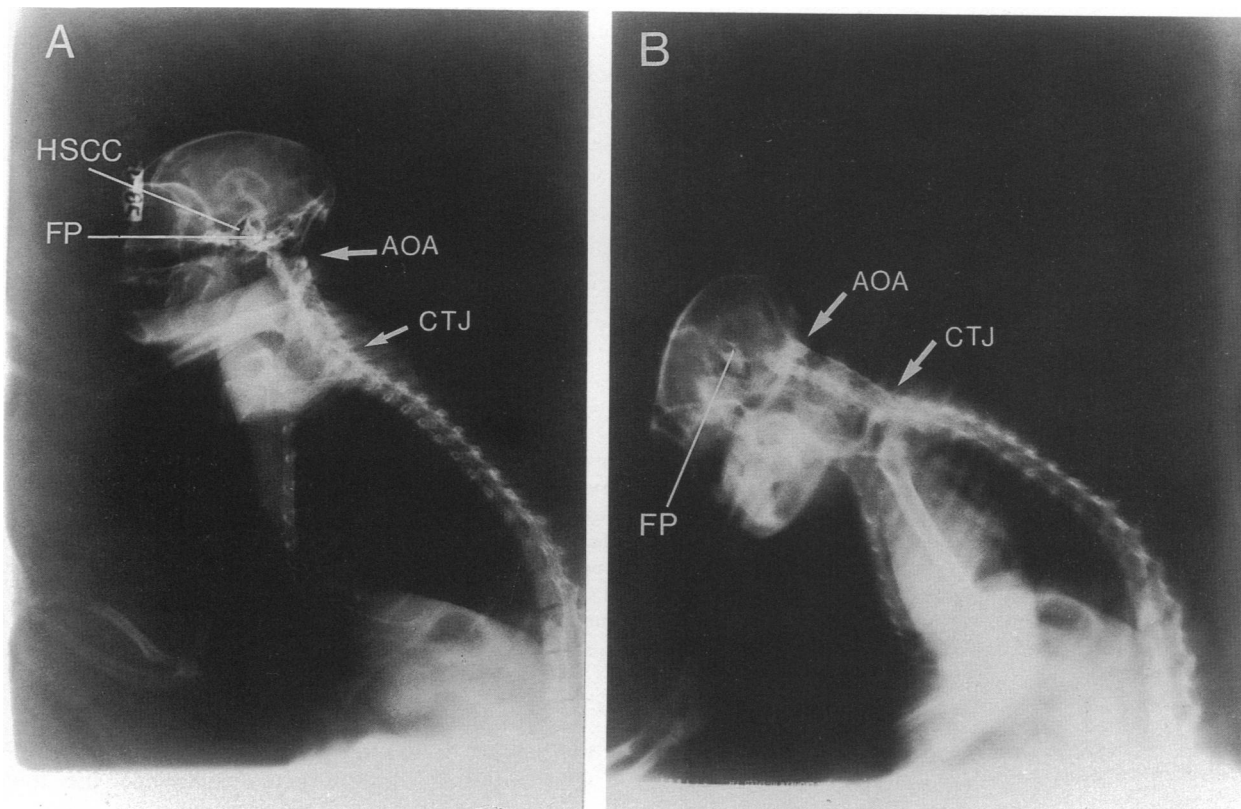


Fig. 9. Lateral radiograph exposure of an alert capucin monkey at rest (A) and during downward gaze (B). Note straight configuration of cervical vertebral column in both instances, and upward tilt of the horizontal semicircular canal plane when at rest (A). For downward gaze, the animal predominantly bends the cervical vertebral column at the cervicothoracic junction, while the atlanto–occipital articulation does not play a large role (compare with Fig. 7, where the rabbit orientates its cervical spine at approximately the same angle as the monkey in B, without effecting any change in resting head orientation). Note that the monkey's head is rotated out of plane in B, making the angle between the Frankfurt plane and the cervical spine appear smaller than in reality. During this active behaviour, the monkey also uses the thoracic vertebral column to some extent to achieve a particular orientation of gaze. AOA, atlanto–occipital articulation; CVJ, cervicothoracic junction; FP, Frankfurt plane; HSCC, horizontal semicircular canal plane.

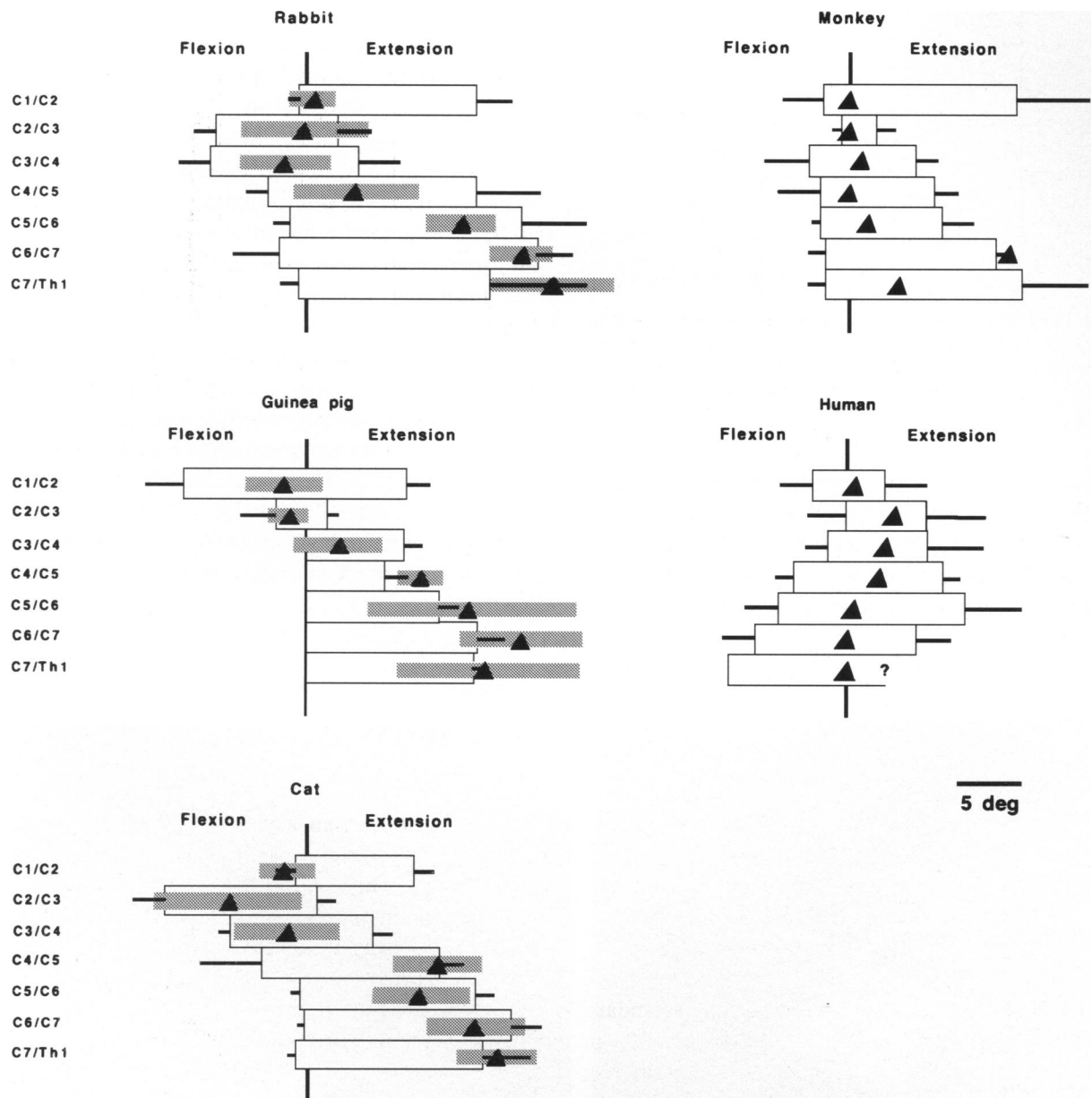


Fig. 10. Comparison of range of motion of the neck joints and their positioning during resting posture in the vertebrates investigated (illustration of numerical values in Tables 2–6). Open horizontal bars symbolise the total ranges of motion of the cervical joints with their respective excursion ranges in the flexion and extension directions as measured against the virtual zero position (vertical solid line). Horizontal solid lines represent 1 s.d. for flexion and extension. Triangles indicate the average flexed or extended attitude for a given cervical joint during the spontaneously assumed resting posture. Stippled bars represent the respective s.d.s. In all instances, except for humans, the upper cervical joints appear in a flexed attitude, whereas the lower ones are positioned at their extreme extension ranges of motion. The transition between flexion and extension occurs at about C3/C4 and C4/C5 in the investigated quadrupeds. In humans, the upper cervical spine appears slightly extended, while the lower cervical vertebrae are held at a midposition between extreme flexion and extreme extension.

### Synopsis

The graphical representations (Figs 10, 11) of the main findings of this study indicate that rabbits, guinea pigs, cats and monkeys hold their head-neck ensembles with the upper cervical joints in a flexed attitude, whereas the lower ones are positioned at their extreme extension ranges of motion. The changeover between flexion and extension occurs at

about C3/C4 and C4/C5. In humans, the upper cervical spine appears slightly extended, while the lower cervical vertebrae are held at a midposition between extreme flexion and extreme extension. Heads are poised such that the horizontal semicircular canal planes are tilted upwards in all instances. Quadrupeds hold their cervical spine close to the gravity vector, whereas bipeds keep a forward leaning attitude of the head-neck ensemble.

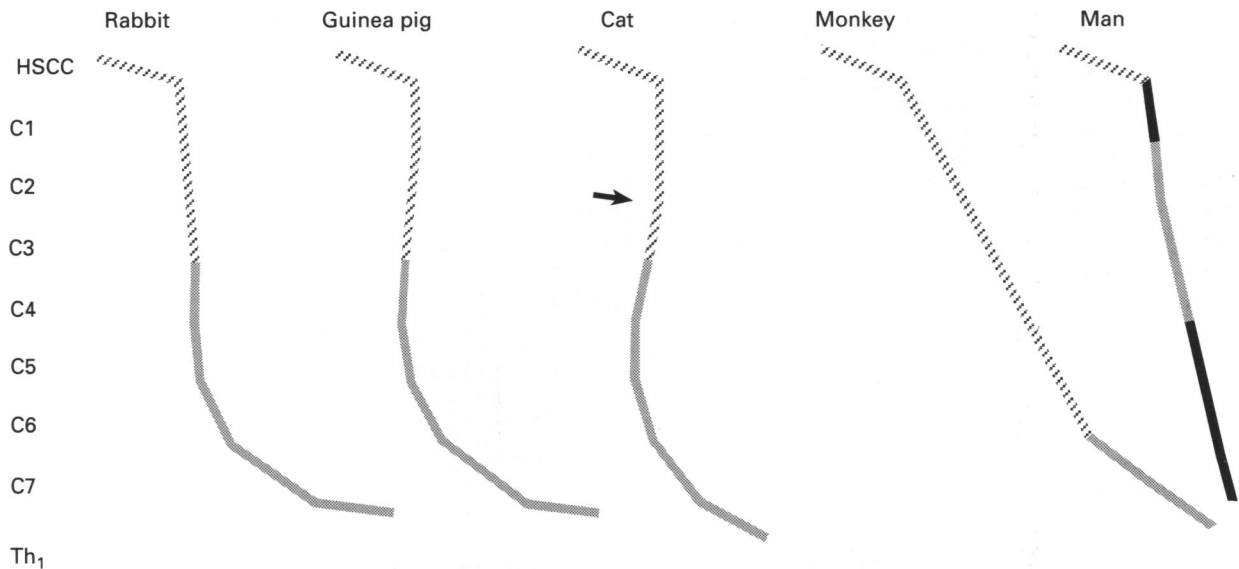


Fig. 11. Global description of the biomechanical characteristics of the head-neck movement system in the investigated vertebrates when at rest (absolute orientations of the head and cervical vertebrae according to the numerical values of Table 7). Note upward orientation of the horizontal semicircular canal plane in all instances. Quadrupeds hold their cervical spine close to the gravity vector; bipeds establish a forward leaning attitude of the head-neck ensemble. At the upper cervical vertebral column, the vertebrae are held at the limits of their flexion range of motion (---); at the middle and lower spine, they are positioned at the limits of their extension range of motion (—). In humans, the 1st and the lower cervical vertebrae are held at about midposition between extreme flexion and extreme extension (—), and the middle cervical column shows a slight extension attitude. Although data are averages of many measurements, the prominent C2/C3 joint in cats is quite noticeable (arrow). This asymmetric placement of the vertebrae in alert animals ensures an energy saving balance of the head when at rest, and provides for the organisation of head orientation movements in privileged planes of space. C1–C7, cervical vertebrae; T1, 1st thoracic vertebra; HSCC, horizontal semicircular canal plane.

## DISCUSSION

At the outset, it should be stressed that noticeable interindividual differences dominated the spread in numerical values of the measured variables of the head-neck articulations in the different vertebrate species. This fact is signalled at times by high standard deviations (see e.g. Tables 2–6 and Fig. 10, in particular for values concerning lower cervical vertebrae). However, general range of motion tendencies could be established and demonstrated by different measurement methods (radiographs and postmortem dissection). We consider the most important finding of our analysis the observation that context-specific interpretations are necessary to describe the functional parameters of a biological system (Graf & Wilson, 1989), even at the biomechanical level. In the specific case of the resting posture of an animal, an asymmetry in the range of motion of particular head-neck joints in the sagittal plane has to be recognised.

### *Intrinsic configuration of the cervical vertebral column*

Our data show that constraints of a mechanical nature most likely by ligaments and bony structures (Fielding, 1957; Adams & Hutton, 1983; Ueno & Liu,

1987) bring about an asymmetric mobility of particular vertebrae into particular directions in the sagittal plane when judged from the resting position. In particular, in quadrupeds, flexion of the head-neck ensemble is largely possible at the lower cervical spine, and head extension can only occur at the upper cervical spine (Fig. 10). This asymmetry is thought to provide structural integrity of the cervical spine and to facilitate control of head movements.

The only moveable joints throughout the cervical column proper that allow noticeable symmetrical excursions from the resting position are vertical axis rotations of the vertebrae relative to one another. Lateral flexion is also symmetric, but quite limited.

It is stressed that we were only able to detect the observed sagittal plane asymmetry, since we separated our range of motion measurements into flexion and extension direction parameters. From these variables, total ranges of motion also could be calculated (see Table 8). These data reveal noticeable excursions of all cervical vertebrae against one another. If only these latter total ranges of motion had been considered (see e.g. the study of Selbie et al. 1993 in cats), the described context-specific asymmetry would have remained unnoticed. The asymmetric placement of the head-neck joints is also quite obvious from our graphic illustration of the ranges of motion under

Table 8. *Averages (mean  $\pm$  S.D.) of total range of motion (deg) of head-neck articulations, and cervical and thoracic vertebral joints in the tested vertebrates as calculated from all original data*

	Rabbit	Guinea pig	Cat	<i>M. fascicularis</i>	<i>S. sciureus</i>	<i>M. mulatta</i>	Man
Head/C1	104.6 $\pm$ 15.7 (11)	106.4 $\pm$ 5.9 (5)	92.0 $\pm$ 14.2 (3)	1.3 $\pm$ 1.5 (3)	18.8 $\pm$ 15.3 (3)	32	11
C1/C2	22.5 $\pm$ 3.3 (6)	39.5 $\pm$ 2.4 (4)	16.0 $\pm$ 3.6 (3)	1.7 $\pm$ 1.5 (3)	16.0 $\pm$ 5.6 (3)	3	5
C2/C3	14.7 $\pm$ 3.5 (6)	5.5 $\pm$ 1.9 (4)	20.0 $\pm$ 4.6 (3)	34.3 $\pm$ 2.1 (3)	5.7 $\pm$ 1.2 (3)	24	5
C3/C4	18.8 $\pm$ 6.3 (6)	13.4 $\pm$ 1.8 (4)	18.7 $\pm$ 2.5 (3)	13.7 $\pm$ 7.0 (3)	13.7 $\pm$ 4.6 (3)	14	9
C4/C5	23.2 $\pm$ 2.8 (6)	10.0 $\pm$ 1.4 (4)	23.7 $\pm$ 5.5 (3)	11.3 $\pm$ 2.4 (3)	15.7 $\pm$ 5.1 (3)	18	12
C5/C6	30.0 $\pm$ 7.7 (6)	17.5 $\pm$ 2.1 (4)	25.0 $\pm$ 6.6 (3)	8.7 $\pm$ 3.2 (3)	16.7 $\pm$ 4.9 (3)	16	26
C6/C7	37.2 $\pm$ 8.1 (6)	—	27.0 $\pm$ 3.6 (3)	16.7 $\pm$ 5.7 (3)	23.0 $\pm$ 1.0 (3)	22	21
C7/T1	25.3 $\pm$ 11.5 (6)	—	24.0 $\pm$ 6.0 (3)	—	31.3 $\pm$ 4.5 (3)	10	20
T1/T2	17.8 $\pm$ 7.9 (6)	—	13.3 $\pm$ 2.1 (3)	—	22.3 $\pm$ 4.7 (3)	26	—
T2/T3	5.6 $\pm$ 2.6 (6)	—	—	—	19.1 $\pm$ 8.1 (3)	1	—
T3/T4	—	—	—	—	12.7 $\pm$ 5.3 (3)	—	—

For rhesus monkeys and man only one set of measurements was entered.

passive and active conditions (Fig. 10). When comparing our respective data with those of Selbie et al. (1993; their table 2), the same tendencies and range of variability are obvious (range of motion of the atlanto-occipital articulation, slightly higher ranges of motion at the lower cervical joints, lower range of motion within the thoracic spine) (Table 8, 3rd column).

The advantage of the demonstrated rigidity of the cervical spine is obvious, taking into consideration that the head needs to be balanced on top of the cervical column. If only muscular structures had to provide this rigidity, the energy-saving aspect of the vertical orientation of the head-neck ensemble would be in question—just imagine how to maintain a rubber garden hose straight and vertical with support from below only! It should be mentioned, however, at this point, that some muscle force will have to be applied, even if only to balance the head-neck ensemble within the gravity vector (see below).

Our radiograph material also suggests that the cervical vertebral column maintains its intrinsic configuration throughout all behaviours. During exploratory behaviour in the rabbit (Fig. 7), when the neck is brought forwards, the cervical vertebral column retains its intrinsic configuration and stiffness. A similar observation can be made in cats even at extreme head positions, e.g. during downward gaze and during eating (Fig. 8). In cats, the C2/C3 joint may be brought into play although the entire functional significance of this articulation is not as yet clear (Fig. 8A).

During upright stance in human bipeds and primate omnipeds, the control problem for head-neck movements is even more exaggerated. The head then protrudes from the trunk without partial embedding into the body profile as is seen in many quadrupeds

(compare Figs 2A, 6A, 9A). Although the entire cervical spine retains its intrinsic configuration, downward gaze in monkeys is only possible by flexing the joints that form the cervicothoracic junction (Fig. 9). We hypothesise that this behaviour is a result of the limited range of motion of the atlanto-occipital articulation in primates (Table 10) necessitating a different movement strategy for head-neck movement control in the sagittal plane (Graf et al. 1995).

A different scenario occurs in man, in whom all lower cervical vertebrae participate in a sliding movement across their curved surfaces. In such a case, a rotation is achieved by means of a translation of vertebrae against one another (see Fig. 6C) (Graf et al. 1990, 1992c; Wang et al. 1991).

It must be stressed, however, that a proper, i.e. upright orientation of the head-neck ensemble including maintaining resting posture, depends on a functioning sensory 'read-out' indicating the direction of gravity (see Graf et al. 1992b). This representation of 'up', the subjective vertical, is the end product of multisensory convergence, consisting of at least vestibular input, vision and proprioception.

#### *C2 orientation in cats*

The special case of the prominent joint between C2/C3 in cats requires further explanation and elaboration since it obviously subserves a function for head-movement control. When assuming alignment between C2 and C3 during resting posture, maximal flexion at this joint averages about 19°, whereas extension is negligible (Table 4). When the C2/C3 joint is engaged to its maximal range of flexion, the angle between the horizontal semicircular canals and C3/C4/C5 will be approximately 90°. Assuming a vertical orientation of the cervical vertebral column

Table 9. *Passive range of motion (deg, mean  $\pm$  S.D.) for lateral flexion in the tested vertebrates*

	Rabbit	Guinea pig	Cat	<i>M. fascicularis</i>	<i>S. sciureus</i>	Man
Head/C1	0	0 (2)	0 $\pm$ 0 (3)	0 $\pm$ 0 (3)	0 (2)	—
C1/C2	12	0 (2)	11 $\pm$ 3.6 (3)	0 $\pm$ 0 (3)	7.5 (2)	—
C2/C3	10	9.5 (2)	2.7 $\pm$ 2.3 (3)	3.0 $\pm$ 3.0 (3)	1.5 (2)	—
C3/C4	11	5 (2)	1.7 $\pm$ 1.2 (3)	2.7 $\pm$ 2.3 (3)	5 (2)	6 (1)
C4/C5	10	3.5 (2)	2.7 $\pm$ 1.5 (3)	8.0 $\pm$ 2.0 (3)	0 (2)	4 (2)
C5/C6	3	0 (2)	0 $\pm$ 0 (3)	7.0 $\pm$ 1.7 (3)	0 (2)	5 (2)
C6/C7	0	0 (2)	1.3 $\pm$ 2.3 (3)	2.7 $\pm$ 2.5 (3)	6 (2)	3.5 (2)
C7/T1	0	0 (2)	0 $\pm$ 0 (3)	—	4 (2)	4 (2)

Limited lateral flexion is only possible at restricted areas. In rabbits only one set of measurements was taken.

(C3/C4/C5), the horizontal semicircular canals will be orientated earth-horizontally in this particular attitude. If the animal assumes a vertically orientation and straight cervical vertebral column configuration (without flexion of C2/C3), the horizontal semicircular canals will be pitched up from earth-horizontal by 20° (Table 7; Fig. 11) when the resting position is achieved. If the cervical vertebral column (C3/C4/C5) remains orientated vertically and only the C2/C3 joint becomes engaged to its maximal extent of flexion, then the horizontal semicircular canals will basically be brought into the earth-horizontal plane. We thus hypothesise that mechanical constraints of the upper cervical vertebral column are used in cats to control the horizontal semicircular canal orientation, e.g. when the level of vigilance changes. The literature maintains that vigilant animals keep their horizontal canals orientated earth-horizontally (e.g. Wilson & Melvill Jones, 1979). Thus, in the transition of a state of rest to a state of vigilance, the pitched up horizontal canal can be brought into the earth-horizontal position simply by flexing the C2/C3 joint to the maximum of its flexion range of motion. Nevertheless, a more detailed analysis of head-neck posture in alert animals is needed to substantiate this hypothesis than could be obtained in our previous (Graf et al. 1995) and present studies.

#### *Functional compartmentalisation*

Our measurements indicate that the cervical and thoracic vertebral column are functionally compartmentalised with regard to the extent and direction of motion, thus allowing movement in the sagittal plane when judged from the resting position. In this scenario, particularly in quadrupeds, 2 asymmetric joints form a unique array to control lowering and raising of the head-neck assembly. Given an 'ideal' resting position of the animal with the cervical

vertebral column oriented vertically, i.e. the direction of the gravity vector, and the head orientated in such a way that the horizontal semicircular canals are slightly pitched up from earth-horizontal (Fig. 11), we find the atlanto-occipital articulation engaged in its maximally active flexed position. In this position, the atlanto-occipital joint will only allow extension of the head (see e.g. Figs 2A, B, 11; Tables 2–6).

In a similar fashion, the joints at the cervicothoracic junction are engaged close to their maximally extended position. Thus only movements in the flexion direction can be performed at the C6–T3 articulations (see Figs 2A, C, 11; Tables 2–6). More specifically, at the resting position, the important joints for flexion-extension of the head-neck assembly, the atlanto-occipital articulation and the cervicothoracic junction, are engaged in their respective end positions of either extension or flexion range of motion, where the least amount of energy has to be expended. Indeed, at the resting position, the animal uses minimal muscle force, activating only biventer cervicis and occipito-scapularis to maintain head-neck posture (de Waele et al. 1988; Richmond & Vidal, 1988; Richmond et al. 1992). It is possible, that this muscle force provides mainly a balance of the head-neck ensemble around the gravity vector.

For head-neck movements in quadrupeds in the frontal plane (side tilt), rotations cannot take place at the level of either the atlanto-occipital joint or at the other articulations of the cervical spine. Since the cervical column can be bent laterally by only a limited extent, any movement exceeding that amplitude has to take place elsewhere. Starting from the resting position, rotations of the upper thoracic vertebrae about their longitudinal axes will lead to an inclination of the whole head-neck ensemble in the frontal plane. This latter finding has been demonstrated by radiographic measurements in guinea pigs (de Waele et al. 1989). In the bipedal humans, this degree of freedom seems to have been lost, when upright stance was

Table 10. Averages of range of motion of the atlanto-occipital articulation across species (deg, mean  $\pm$  s.d.)

Rabbit	104.6 $\pm$ 15.7	(11)
Guinea pig	106.4 $\pm$ 5.9	(5)
Cat	92.0 $\pm$ 14.2	(3)
Monkey	13.0 $\pm$ 14.2	(7)
Man	11	(1)
	25	(White & Panjabi, 1990)
	8–13	(Dvořák, 1988)

Note large ranges of motion in quadrupedal mammals, and significant reduction of mobility in primates. Data from humans come from our own measurements and from published material.

achieved via an erect spinal column. Longitudinal axis rotations of the upper thoracic vertebrae now will only effect a horizontal rotation of the head, but no longer a side tilt of the entire head-neck ensemble.

#### *The atlanto-occipital articulation*

In monkey and man, the range of motion of the atlanto-occipital articulation is relatively small compared with quadrupeds (Table 10). The reduced range of sagittal motion at the atlanto-occipital joint in higher primates may reveal some principles as to how animals locomote and how they control their posture in light of the different requirements for quadrupedal versus bipedal stance.

In quadrupedal animals, the cervical spine is a vertical part of the entire vertebral column (Fig. 2A). In this configuration, the thoracic column is orientated more or less horizontally. Thus, in the sagittal plane, movement of the head-neck ensemble is operated and controlled by 2 functional joints, the atlanto-occipital articulation and the cervicothoracic junction (Graf et al. 1995). In permanent or temporary bipedal mammals such as man and monkeys, the entire spine assumes a general vertical orientation and its curvatures are much less pronounced (see e.g. Tobias, 1983, 1992). Consequently, the neck protrudes from the top of the trunk in bipedal mammals (Figs 6A, 9A) and presents an entirely different motor control problem with respect to gravity. Thus the necessity for independent control of 2 functional joints may have become a phylogenetic disadvantage, since when in this position, a single controllable joint unit will suffice. As a possible consequence, the degree of freedom represented by the atlanto-occipital articulation largely disappeared.

#### *Conclusions*

The overall goal of our work was to demonstrate functional principles of head movement control specifically, and motor control more generally, that are common to vertebrates. In this context, Bernstein (1947) has proposed that certain movement axes may have become prevalent during motor activity when multiarticular segments of the body needed to be coordinated. Our data from quadrupedal and bipedal mammals indicate that particular head-neck movements are indeed confined to privileged planes in space, at least for sagittal-plane movements. At the upper cervical vertebral column, vertebrae are held at the limits of their flexion range of motion only allowing extension. At the lower spine, they are positioned at the limits of their extension range of motion, only allowing flexion. This general asymmetric placement of the vertebrae in alert animals also ensures an energy-saving balance of the head when at the resting position. In the special case of humans, the lower cervical vertebrae are held at about midposition between extreme flexion and extreme extension. It remains to be determined whether this observation is directly related to the permanent bipedalism and upright stance of humans.

Vestibular input, providing one sensory modality for postural control mechanisms, also seems to be separated according to the biomechanical compartmentalisation. Semicircular canal afferents converge on neck muscles that control the atlanto-occipital articulation and the atlanto-axial joint. Otolithic inputs largely control antigravity muscles of the cervicothoracic junction (de Waele et al. 1989; Graf et al. 1992b).

The observed postural asymmetry and reduction in the degrees of freedom point to an important principle of brain operation—mechanical and physiological constraints are used as much as possible to reduce the degrees of freedom that need to be controlled by the nervous system (see also Simpson & Graf, 1985; Graf, 1988). When comparing quadrupedal and bipedal mammals, the qualitative constraints inherent in the head-neck movement system are further enhanced in bipeds by quantitative modifications at the atlanto-occipital articulation that almost remove one degree of freedom from the system. One additional reduction in degrees of freedom occurs by the functional loss of longitudinal axis rotation of upper thoracic vertebrae to achieve lateral head tilt after the thoracic vertebral column assumed a vertical orientation in bipeds. In this context, aspects of brain-to-body ratio, movement economy and phylogenetic constraints must be

considered (Gould, 1977; Grüsser & Weiss, 1985) and the described reductions in degrees of freedom viewed in regard to the evolution of vertebrates.

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